Fallacies Underlying the Assumption of Calcium Limitation on the Evolution of Land Snails in Bermuda

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Abstract. The supposed lack of calcium during glacial periods of red soil development has been cited as the principal factor influencing evolution in land snail shells on Bermuda during the Quaternary. We argue that at no time was there an appreciable deficiency of calcium carbonate on Bermuda because the red soils themselves are largely made up of carbonate and because calcium in plant tissues would have been recycled during all stages of the Quaternary by frequent forest fires. Supposed instances of very localized changes in shell thickness arose through misinterpretation of chronology. Paedomorphic populations of the subgenus *Poecilozonites* occur only in carbonates of the last interglacial (Marine Isotope Stage 5) and the Holocene, never in glacial red soils as maintained repeatedly by Gould.

INTRODUCTION

In several studies, Gould (1966, 1968, 1969, 1970a, b, 1971a, b) investigated evolutionary trends in diversity of shell size and shape in land snails, particularly of the genus *Poecilozonites*, subgenus *Poecilozonites* (Zonitidae), on the remote, oceanic island of Bermuda. He repeatedly hypothesized that the lack of calcium carbonate during glacial episodes, when snails were supposedly living on lime-poor red soils, was of prime importance in driving evolution in Bermudan snails.

In attempting to explain repeated instances of paedomorphosis in the subgenus *Poecilozonites*, Gould (1968: 81) stated that: "The most paedomorphic subspecies originated in red soils; paedomorphs did not evolve in times of carbonate-dune deposition. The thin shells of paedomorphs might have been adaptive in the low-calcium environment of red soils." Gould (1977: 277) later unequivocally identified the "adaptive trigger" of paedomorphosis as "the almost totally lime-free soils that served as substrate for the most paedomorphic forms."

Calcium-poor red soils supposedly not only explained paedomorphosis but also influenced evolution in other lineages in the subgenus (Gould, 1969: 482–492). For example, in the giant species *P. nelsoni* "a thin-shelled subspecies lived in red soils" (Gould, 1969: 491).

In another study, Gould (1970a: 572) proposed that variations in relative abundance or shell morphology in six different species or populations of land snails on Bermuda during the last two glacial cycles "was influenced primarily by the availability of calcium carbonate for shell construction."

And in yet another case (Gould, 1971a: 91), what were interpreted as very restricted local populations of several different snails were thought to differ from their supposed contemporaries elsewhere in the island because of local soil conditions, thus providing support for Gould's "previous assertion (Gould, 1968 and [1969], pp. 482–483) that the adaptive significance of paedomorphosis ... lies in the thin shell that it produces and that lime-poor habitats require."

A much more refined knowledge of the stratigraphy and geochronology of Bermuda (e.g., Vacher et al., 1989, 1995; Hearty, 2002; Hearty et al., 2004) than was available to Gould presents a very different picture of the evolution of the island's snails. The progress achieved in unraveling the complex limestone architecture of Bermuda's sedimentary units and their ages can be partially attributed to traditional and new applications of amino acid racemization (AAR) geochronology (Hearty et al., 1992). We have determined the degree of epimerization of D-alloisoleucine/L-isoleucine (or A/I) from several populations of *Poecilozonites* including *P. bermudensis bermudensis*, *P. b. fasolti*, and other paedomorphs (Tables 1 and 2). AAR geochronology provides an independent means with which to determine relative ages and age-succession of the land snails in question. A/I is determined on several individual snails from each sample. A/I values are approximately 0.015 in living specimens, 0.40 to 0.58

Table 1

Taxa of *Poecilozonites* (*Poecilozonites*) discussed in this paper with their old and revised chronologies. Each of the main lineages (*P. b. bermudensis*, *P. b. zonatus*, and *P. nelsoni*) was considered by Gould (1969) to be continuous across their age ranges. The stratigraphic names used in Gould (1969) are poorly defined in terms of both stratigrapic position and apparent age (see Hearty, 2002). We offer only inferences of what Gould may have meant by use of these stratigraphic names.

Taxon	Old chronology (ages inferred from Gould, 1969)*	Revised chronology (estimated age ka) This study	Correlated marine isotope stage (MIS)	Comments
P. b. bermudensis (Pfeiffer, 1845)	St. Georges, Southampton, Recent (80 ka to present?)	Holocene (12 ka -present)	MIS 1 only	The modern phyletic lineage evolved independently of paedomorphs in the Pleistocene.
P. b. zonatus (Verrill, 1902)	Shore Hills (>300 ka?) to St. Georges (80–10 ka?)	Interglacial intra-dune and post highstand soils (130–80 ka)	All MIS 5 only	Considered to be the trunk species of all *P. bermudensis*
P. b. fasolti (Gould, 1969)	Shore Hills (>300 ka?)	Holocene cave colluvium (1–2 ka)	Late MIS 1	Differs only slightly from other late Holocene morphotypes
P. b. siegmundi (Site 6; Ireland Isl.) (Gould, 1969)	Harrington red soil (post 125 ka?)	Interglacial intra-dune soils (c. 100–115 ka)	Mid MIS 5	AAR ratios indicate *P.b. siegmundi* and *P.b. sieglindae* are the same mid MIS 5 age
P. b. sieglindae (Site 5; Rocky Bay) (Gould, 1969)	Pembroke and Harrington red soil (post 125 ka?)	Interglacial intra-dune soils (c. 100–115 ka)	Mid MIS 5	Two additional unnamed last interglacial age paedomorphs are of similar (St. Georges), or slightly older ages (Hamilton) compared to the named subspecies
P. nelsoni (Bland, 1875)	Shore Hills (>300 ka?) to St. Georges (80–10 ka?)	Glacial red soils (180–130 ka and 80–10 ka)	MIS 6, 4–2	Nearly identical *P. nelsoni* morphotypes are found in three successive glacial-age soils

from shells from Marine Isotope Stage (MIS) 5 (last interglacial), and progress to an equilibrium ratio of 1.30 after perhaps 1,000,000 yr (Hearty et al., 1992). With independent ^{14}C or U/Th age calibration at key intervals in the epimerization reaction, it is possible to compute absolute age estimates directly from A/I. Relevant discussion and protocols regarding this application and underlying database are available in Hearty et al. (2004).

Before detailing evolutionary sequences and the possible causes in subsequent papers, we wish to dispose of the fallacious assumptions and erroneous facts associated with the hypothesis of the effects of carbonate limitation on the evolution of Bermudan snails. It is highly unlikely that any significant area of Bermuda was deficient in calcium at any period during the entire post-volcanic history of the island. In one lineage, snails during glacial periods deposited far more calcium in their shells than during interglacial times. Gould's (1971a) instance of highly local environmental control was based on an erroneous assumption of the

age of the sample. And finally, in complete contrast to Gould's repeated assertions, all of his fossil examples of paedomorphs existed during interglacial times of high carbonate deposition and never occur in glacial red soils.

AVAILABILITY OF CALCIUM ON BERMUDA

To begin with, Gould's correlation of shell variation with the amount of calcium carbonate in the substrate is compromised by Goodfriend's (1986) detailed review of causes of variation in shells of land snails. Gould (1968) cited investigations by Rensch (1932) and Oldham (1934) as showing calcium deprivation to result in shell thinning or mortality in snails. Yet the same papers are cited by Goodfriend (1986: 208) as finding ambiguous results for a correlation between shell size and limestone availability. Goodfriend (1986: 208) concluded that field studies "failed to reveal any relationship between shell size and the calcium-

Table 2

Amino acid ratios on *Poecilozonites b. bermudensis (Pbb)*, *P. b. fasolti (Pbfas)*, *P. b. sieglindae* (Pbsl), *P. b. siegmundi* (Pbsm) and unnamed paedomorphs (paed) from Bermuda. Gould (1969) collections from the MCZ are identified by "SJG" prefix. Our collections from numbered Gould (1969) sites are preceded by our field number, then Gould's. NAU-AAL = sample number from Northern Arizona University Amino Acid Laboratory. Age interpretations not in years refer to Marine Isotope Stage (1 = Holocene; 5 = last interglacial). Gould's Tom Moore's Cave is thought to be the same as either Walsingham Cave or Walsingham Sink Cave. The date for Fern Sink Cave is based on a charcoal AMS ^{14}C age of 1630 ± 60 yr BP (Hearty et al., 2004).

Site # Fig. 1	FMNH	NAU-AAL	FIELD #	Spp	Locality information	Age/Interp.	Mean	St Dev	N=
—	—	4081	ANSP 85510	Pbb	Alive 1903	104 yr	0.017	0.001	1
2	303192-3	3841	SJG53	Pbfas	Tom Moore's Cave *P. b. fasolti* (Gould's collection)	Late 1	0.055	0.034	2
2	303194-5	3847	UGC1z(2a)	Pbb	Fern Sink Cave upper	1,630 yr BP	0.047	0.014	3
2	303196	4575-77	UWV1	Pbb	Walsingham Cave	Late 1	0.045	0.017	3
2	303197	4578-80	UWS1	Pbb	Walsingham Sink Cave, entrance	Late 1	0.046	0.019	3
2	303198	4403, 05	UWSu2	Pbb	Walsingham Sink Cave, deeper deposit	Late 1	0.069	0.008	2
2	303199	3845	UGC1x(2)	Pbb	Fern Sink Cave lower level	Mid 1	0.097	0.023	3
7	303200-1	4607-10	UTB1/2	Paed	Tobacco Bay, St. Georges	Late 5	0.40	0.03	3
5	303202-4	790514.1	URB–SJG 44	Pbsl	Rocky Bay, type *P. b. sieglindae*	Mid 5	0.51	0.01	2
6	303205-8	3838-29	UII1- SJG10	Pbsm	Ireland Island, type *P. b. siegmundi*	Late 5e	0.523	0.027	6
8	303209	3837	USL1d	Paed	Shell Depot	Late 5e	0.542	0.05	3
9	303210	3864	USS1c	Paed	Saltus School, 1989	Mid 5e	0.587	0.021	3

carbonate content of the substrate" and that "experimental studies give similarly inconsistent results."

But it is one thing to suggest that lime-poor soils drive snail evolution and another to show that snails on Bermuda ever experienced lime-poor soils. The island of Bermuda (Figure 1) is composed almost entirely (over 95% of surface rocks) of lithified dunes of calcium carbonate sand formed from skeletal remains of marine invertebrates and coralline algae. Dune deposition takes place during interglacial periods when sea levels are elevated (Bretz, 1960). During the depressed sea levels of glacial periods, when the entire

Figure 1.   Location map of sites discussed in the text.

Bermuda platform is exposed, marine carbonate supply is cut off and red soils form from diagenesis of limestone and from wind-borne dust (Bricker & Mackenzie, 1970; Muhs et al., 1990), which is more abundant in the atmosphere and polar ice during glacial periods (Glacuum & Prospero, 1980).

Because they are developed directly on limestone, most soils on Bermuda contain large amounts of calcium carbonate ($CaCO_3$), often in the form of carbonate sand or silt. Of the 45 samples in 9 soil profiles analyzed by Ruhe et al. (1961: their tables 3, 4), 41 were more than 80% $CaCO_3$, and only 4 were below 14.6% (all from subsurface horizons in the more ancient soils). The upper and surface samples in each profile were all above 63% $CaCO_3$. All levels in the deep deposits of Admirals Cave, which span the past 120 kya and thus include both glacial and interglacial slope wash sediments, contain at least 70% $CaCO_3$ (Hearty et al., 2004).

The thickest soil development on Bermuda occurred during a prolonged period of depressed sea-levels from about 800 kya to 450 kya—the Big Red Soil of Hearty et al. (2004) and Olson et al. (2005). No specimens of land snails are known from this period and all of those studied by Gould are younger. Regardless, it is unlikely that snails in Bermuda ever lived on soils that were substantially lacking in calcium.

Even during glacial periods when red soils develop, areas of high relief and any erosional features would expose bare carbonates, particles of which would be carried by wind or water to places where carbonates are
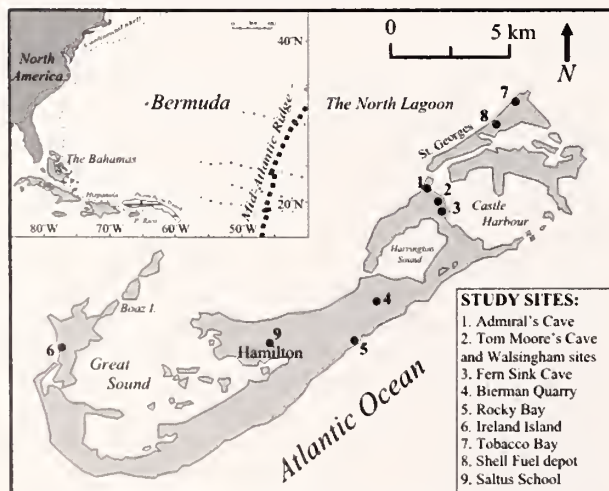
covered by soil. Furthermore, snails need not derive calcium directly from the substrate, as they would also obtain substantial amounts of calcium from plant detritus. Calcium is necessary for the formation of plant cell walls, where once incorporated it remains inert. Thus it is necessary for new growth, so that plants themselves would not thrive on truly calcium deficient soils. If there actually were local areas where soils were deficient in calcium, these would nevertheless receive calcium from plant detritus blowing from areas higher in $CaCO_3$ and from $CaCO_3$ dust from the shore and erosional features exposing limestone.

The roots of larger plants on Bermuda such as palmetto (*Sabal bermudiana*) and particularly cedar (*Juniperus bermudiana*) would be able to penetrate soils to take up calcium directly from underlying carbonate deposits. Calcium sequestered in plant tissues such as dead leaves, bark, and wood, would be released in ash after burning. Bermuda experienced numerous natural fires probably throughout its history. We found charcoal, sometimes in great quantity, throughout the entire sequence in Admirals Cave (location in Figure 1) representing the last 120 ky of Bermuda's history (Hearty et al., 2004). We have also seen evidence of extensive natural burning in glacial soils of MIS 10 (about 300 ± 30 ky old) exposed in Bierman's Quarry (location in Figure 1; see Olson et al. 2005 for information on this site). Thus, there were fires capable of releasing calcium stored in plant tissues throughout the entire the fossil record that Gould studied. In short, it is difficult to imagine any situation in which a Bermudan snail would be stressed to obtain sufficient calcium for shell building.

TOTAL SHELL CARBONATE in GLACIAL VERSUS INTERGLACIAL SNAILS

It was Gould's (1969: 487) contention that "snails from red soils (glacial periods) tend to reach larger maximal sizes, have thinner shells and be smaller at a whorl than samples from eolianites." Shell thinning was supposed to be an indication of decreased calcium resources. But in none of his writings on the subject did Gould provide any quantitative measures of shell thickness or mass of Bermudan snails.

If calcium carbonate were ever a limiting factor in snail evolution in Bermuda we would expect this to be reflected in the total shell mass, regardless of thickness. From our excavations in the finely stratified deposits in Admirals Cave and from dating of specimens from many other sites around the island, we can now be quite confident about the sequence of shell forms in the subgenus *Poecilozonites* since the penultimate glaciation (Hearty et al., 2004). The last two glacial periods are characterized by the presence of the giant form known as *P. nelsoni*. Although this form evolved

independently in each of these glacial episodes, the forms are identical in size and shape so far as we have been able to determine. During the last interglacial, the widespread and abundant *P. b. zonatus* prevailed, and *P. b. bermudensis* characterized the present, Holocene, interglacial, although it is now perhaps extinct (Bieler & Slapcinsky, 2000). A sample of 10 shells of *P. nelsoni* had a mass of 37.7 g, whereas 10 shells of *P. b. zonatus* weighed 10.2 g, and 10 shells of fully mature individuals of *P. b. bermudensis* weighed 7.4 g, whereas 10 from a lot of smaller shells weighed 5.0 g. Although these are pretty simple statistics, additional data are not going to alter the fact that in this lineage of *Poecilozonites* individual snails were depositing 4 to 5 times as much calcium in their shells during glacial periods as their successors did during interglacials. This does not support Gould's idea of a deficiency of calcium carbonate during glacial periods.

A CASE of "UNUSUAL PRECISION" of ENVIRONMENTAL CONTROL NEGATED

Gould (1971a) cited a sample containing five species of snails from what he believed to be a Pleistocene red soil deposit (his "Shore Hills Soil") at a site that he called Tom Moore's Cave as being an example of an "extremely local event" in which very tight environmental control was exerted on shell morphology. In all five species the umbilical widths were greater than in "contemporaneous" samples from elsewhere on the island, meaning those that were also believed to be derived from the Shore Hills Soil.

The large umbilicus was said to be negatively correlated with shell thickness (i.e., shells were thinner), which in turn was believed to be a response to low $CaCO_3$ levels in the soil. Thus, supposedly, over a small area of lime-deprived soil, all five species developed thin shells and large umbilici, whereas their supposedly contemporaneous nearby neighbors with greater availability of lime did not. What Gould did not mention, however, is that the snails from Tom Moore's Cave are also exactly like the modern representatives of the same species.

The greatest error to which Gould was subject in his studies of Bermudan snails was his belief that all samples from caves and fissures, which were associated with red soils, came from what he regarded as a middle Pleistocene Shore Hills Soil (Sayles, 1931) and were broadly contemporaneous. We now know, however, that snails and their enclosing soils in fissures and caves are not all contemporaneous. This is explained by the sedimentary process of fissure and cave filling. As a "pitfall" void opens to the surface, the capping soils on the host limestone, which may be hundreds of thousands of years old depending on the formation, would fill the void. In addition, organisms living at the

Table 3

Simple morphometric data from Bermuda *Poecilozonites* paedomorphs discussed in this study. Rows in **bold** are from Gould's MCZ collections, and in plain type from our (O&H) field collections of Gould's and other relevant sites. Morphometric measures of Gould's (1969) *P. b. fasolti* (SJG53) and our sites from Walsingham Cave (UWV1) and Walsingham Sink Cave (UWS1) show no significant differences. With the exception of UCG1x, *P. b. fasolti* and our samples are statistically identical in size and shape. On the basis of morphometric and amino acid data, we are confident that we are dealing with the same populations as described in Gould (1969) and that *P. b. fasolti* is late Holocene and the same as *P. b. bermudensis*.

Gould (1969) samples our collections (O&H)	Shell width (mm)	±1σ	Shell height (mm)	±1σ	Height/Width	±1σ	Total size (w + h, mm)	±1σ	N
SJG53 *P. b. fasolti*	**21.76**	**1.26**	**8.51**	**0.38**	**0.40**	**0.02**	**30.26**	**1.56**	**5**
(O&H) *P. b. fasolti*	21.82	1.26	8.53	0.62	0.39	0.02	30.35	1.78	40
(O&H) UWV1 *Pbb*	21.86	0.81	8.60	0.66	0.39	0.03	30.46	1.28	15
(O&H) UWS1 *Pbb*	21.91	1.73	8.49	1.08	0.39	0.03	30.41	2.71	15
(O&H) UGC1z (1) *Pbb*	21.76	2.43	8.76	1.62	0.40	0.03	30.51	4.00	7
(O&H) UGC1x (2) *Pbb*	19.15	1.40	7.43	0.87	0.39	0.02	26.58	2.20	6
P. b. bermudensis	**20.05**	**5.44**	**7.40**	**1.27**	**0.37**	**0.04**	**27.45**	**6.72**	**2**
(O&H) Holocene *Pbb*	19.33	1.67	7.30	2.09	0.40	0.03	27.04	1.84	175
(O&H) Pleistocene "*Pbb*"	19.52	. 1.28	7.68	0.62	0.39	0.02	27.19	1.82	30
All paedomorphs	**22.03**	**0.81**	**8.13**	**0.40**	**0.37**	**0.02**	**30.17**	**0.85**	**3**
P. b. siegmundi (Pbsm)	**21.90**		**8.50**		**0.39**		**30.40**		**1**
(O&H) *Pbsm*	21.40	1.03	9.67	0.60	0.45	0.02	31.07	1.46	6
(O&H) *Pbsm*	20.93	2.57	8.53	2.03	0.40	0.05	29.47	4.60	3
P. b. siegliudae (Pbsl)	**21.30**		**7.70**		**0.36**		**29.00**		**1**
(O&H) *Pbsl*	21.80		7.60		0.35		29.40		1

surface that succumb to the same pitfall would also be mixed with the ancient soils. This diachrony, explained in Hearty et al. (2004), was clearly not understood by Gould, leading to grave misinterpretation of the biostratigraphic succession of *Poecilozonites*. Snails that Gould assumed were from his Shore Hills Soil, which he thought to be between 0.3 to 1 million yr old (MIS 9 to ~25), include specimens from the last two glacial episodes (MIS 6 and 4/2), the intervening interglacial (MIS 5), and the Holocene (MIS 1) (Hearty et al., 2004).

We have not been able to determine with absolute certainty which of several caves near Tom Moore's Tavern is the one from which Gould obtained his sample, but from our reconnaissance of the area it is most likely that this cave was one of two now known as Walsingham Cave and Walsingham Sink Cave (Olson et al., 2005), probably the latter. In Walsingham Cave the fossils in sediments that we found were entirely Holocene in age. In Walsingham Sink Cave, both in a rockshelter at the entrance and in a more extensive deposit deep in the cave, a thin veneer of loose Holocene sediments (by the inclusion of *P. b. bermudensis*) rested unconformably on a deeper, more compacted soil deposited during the last (Wisconsinan – MIS 2–4) glacial stage, as determined from the inclusion of *P. nelsoni* and the flightless rail *Rallus recessus* (Olson & Wingate, 2001; Hearty et al., 2004; Olson et al., 2005).

Regardless of the precise identity of Gould's Tom Moore's Cave, we have measured and analyzed a sample of Gould's *P. bermudensis fasolti* from his own collection (SJG site #53; Gould, 1969: p. 507) at the MCZ (Tables 2 and 3). Two shells of *P.b. fasolti* yielded a mean AAR ratio of 0.055 ± 0.034. Although we have no independent ^{14}C ages for these specimens, a single *P. b. bermudensis* shell from nearby Fern Sink Cave (UGC1z) produced a mean ratio of 0.047 ± 0.014 (3) with an AMS ^{14}C age of 1,630 ± 30 yr BP (Table 2). The estimated age of Gould's sample of *P. b. fasolti*, based on the age of the Fern Sink sample (Hearty et al., 2004; and Figure 2), is 1900 ± 1200 yr. The late Holocene age of the Tom Moore's Cave sample is unquestionable; the larger error being the result of the limited number of shells analyzed. Additional samples from Walsingham Cave (UWV1) and Walsingham Sink (UWS1) caves gave similar mean A/I values and morphometry (Tables 2 and 3). At this very rapid early stage of the epimerization reaction, small differences in age (i.e., several hundred years) would result in significantly different A/I ratios. Because the method is destructive we chose to limit the number of shells damaged by sample extraction.

To summarize, the sample of snails that Gould (1971a) attempted to use to show "unusual precision" of environmental control in the middle Pleistocene is actually late Holocene in age, only 2 ± 1 ky old, and is
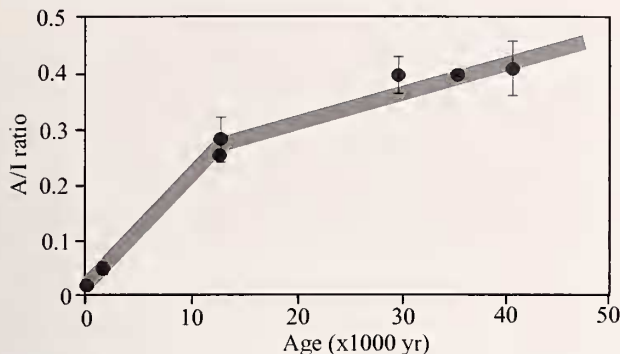
Figure 2. Accelerator mass spectrometry (AMS) ^{14}C calibration of *Poecilozonites* epimerization history over the past 40 ka (Hearty et al., 2004). All samples older than 10 ka are *P. nelsoni*, which has demonstrated a slightly faster (1.2×) epimerization rate than *P. bermudensis*, or *P. b. zonatus*.

thus essentially modern in all respects. It tells us no more about evolution than any other modern sample.

THE SOILS ON WHICH PAEDOMORPHS ORIGINATED

Gould (1969) interpreted several populations of *P. bermudensis*, including the modern nominate subspecies, as paedomorphic offshoots that evolved independently at least 4 different times from non-paedomorphic stock. We agree with some aspects of this interpretation, namely that the forms are paedomorphs and that they evolved independently more than once. We will deal with the evolution of paedomorphs in another paper but here intend to take a closer look at Gould's extraordinary statement that the paedomorphs "originated in red soils; paedomorphs did not evolve in times of carbonate-dune deposition" (Gould, 1968: 81).

The modern taxon *Poecilozonites bermudensis bermudensis* was Gould's prime example of a paedomorph. This form occurred throughout the island in historic times, although it was apparently extirpated in the 20th century by introduced predators and other human-induced environmental factors. We now know that *P. b. bermudensis* evolved very rapidly at the beginning of the Holocene (Hearty et al., 2004), so it never existed in a glacial environment, or during a glacial episode. The Holocene is an interglacial episode with high concentrations of carbonates at the surface, although few of these surface carbonates are of Holocene age.

Gould (1969: 480, fig. 20) thought that his *P. b. fasolti* was the earliest of the various paedomorphic offshoots, supposedly originating in the red middle Pleistocene "Shore Hills Soil." As discussed above, however, topotypical paratypes of *P. b. fasolti* (SJG #53) are only 2 ± 1 ky old, hence essentially modern. Thus *P. b. fasolti* becomes a synonym of *P. b.*

bermudensis and is not associated with a glacial period or glacial soils.

We collected new material from most of the other sites in which Gould identified paedomorphs as well as in several additional sites that we discovered. We determined A/I ratios from this new material and also from Gould's original material stored at MCZ. As detailed below, all of these paedomorphs occurred in sand or protosols of various stages of the last interglacial (MIS 5).

Two other paedomorphic forms that Gould (1969) named, *P. b. siegmundi* and *P. b. sieglindae*, were both considered by Gould to come from what was then called the Harrington Formation, which in Gould's own sequence (1969: 414, tab. 1) was attributed to the last interglacial period, thus directly contradicting his assertion that paedomorphs originated in glacial red soils. We collected topotypes of *P. b. siegmundi* on Ireland Island (Gould's site 10) from what we agree is a post-peak last interglacial (MIS 5e) highstand unit. These occurred in a white structureless, nearly pure *carbonate* 'protosol' (Vacher & Hearty, 1989) such as form during interglacials during pauses in eolian deposition when vegetation colonized dunes, and soils began to form. The incipient soil development ceased when renewed eolian activity buried the horizon. Mean A/I ratios of 0.52 ± 0.03 (n = 6) at Ireland Island confirm that deposition followed shortly after the peak MIS 5e highstand, not during a glacial episode and with no red soil.

Similarly, the type locality of *P. b. sieglindae* at Rocky Bay (Gould's site 44) is a protosol immediately overlying Devonshire marine deposits. A/I ratios of 0.51 ± 0.01 (n = 2) are equivalent to those of the Ireland Island paedomorphs, placing this taxon in the MIS 5 interglacial. Once again, no glacial period, no red soil.

Paedomorphs occur in MIS 5 interglacial deposits at several other sites as well. Samples that Gould (1969: 515) identified as *P. b. bermudensis* from his sites 11, 12, 15, 16, 21, 24, and 27 probably all fall in this category. These must therefore have evolved independently of *P. b. bermudensis*, which did not originate until the Holocene (Hearty et al., 2004). We have found two new sites near Saltus School in Hamilton and at the Shell fuel depot in St. Georges (probably the same rock unit as Gould's site 11) that yielded A/I mean values of 0.59 ± 0.02 (n = 3) and 0.54 ± 0.05 (n = 3), respectively. These values would place the paedomorphs at, or shortly after, the peak of the last interglacial (MIS 5e). Our sites increase the number of last interglacial deposits yielding paedomorphs, and extend their geographic range to central and eastern localities in Bermuda (Figure 1). Paedomorphs at Tobacco Bay (Gould site 27), also in St. Georges, occur in a protosol, but in this case are associated with

late MIS 5 interglacial Southampton eolianites, thus being somewhat younger than the others mentioned above. A/I from the site is 0.40 ± 0.03 (n = 3), which is correlated with the peak of the Southampton marine transgression and associated highstand sediment flux on to the island (Vacher & Hearty, 1989; Hearty et al., 1992).

In summary, all Pleistocene paedomorphs of the subgenus *Poecilozonites* occur in nearly pure carbonate (>95%) soils in deposits of the last interglacial (MIS 5). Those from the current interglacial (Holocene) occur in surface and pitfall deposits with high carbonate content (>70%). Whatever the cause may be for their paedomorphosis, it was not a result of living on "the almost totally lime-free soils" of glacial episodes (Gould 1977: 277).

CONCLUSION

A revised and much more accurate and detailed chronology of the geological deposits in which fossils occur now presents a very different picture of evolutionary sequences and events in the history of snails on Bermuda from anything envisioned by Gould. Changes in shell size and shape through the Pleistocene were rapid, repeated, and dramatic. While this new context for understanding change in Bermudan land snails should prove more instructive of evolutionary patterns than before, the underlining causes may be more difficult to discern. Calcium limitation was the only cause that Gould advanced and it became for him, to use one of his pet phrases, a *deus ex machina*. We believe that lack of sufficient calcium was probably the last problem any snail on Bermuda would ever have to face, so that other explanations will be required.

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